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**ON SOME ASPECTS OF ECOLOGICAL RESILIENCE
AND THE CONSERVATION OF SPECIES**

by

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AND THE CONSERVATION OF SPECIES**

Amitrajeet A. Batabyal

ABSTRACT

The importance of the notion of resilience in determining the static and the intertemporal behavior of jointly determined ecological/economic systems has been recognized by ecologists at least since Holling (1973). This notwithstanding, there are very few formal studies of such systems that explicitly analyze the ecological *and* the economic aspects of the problem. Consequently, this paper has two objectives. First, a new stationary probability-based method is proposed to characterize the notion of ecological resilience. Next, this characterization is used to study the problem of optimal species conservation.

Key words: resilience, species conservation, stationary probability

ON SOME ASPECTS OF ECOLOGICAL RESILIENCE AND THE CONSERVATION OF SPECIES¹

1. Introduction

In recent times, a consensus has emerged among ecologists and economists that if the general process of economic development is to be sustainable, then it will be necessary to conserve at least some environmental resources. The decision as to how many and which species to conserve is closely related to the notion of substitutability; in particular, to two kinds of substitutability. The first kind concerns the substitutability between natural and produced capital, and the second kind concerns the substitutability between different kinds of natural capital. As far as this second kind of substitutability is concerned, economists now generally agree that it is not reasonable to assume that environmental resources that are substitutes in terms of consumption are also substitutes in terms of their ecological functions. Nevertheless, as Perrings (1996, p. 232) noted, “. . . the complementarity between species in many ecosystems is still very imperfectly understood.”

This interspecies complementarity is important because the *resilience* of ecological functions in most terrestrial ecosystems is an increasing function of the number of substitute species that can perform those functions (Schindler 1990; Holling 1992). A perusal of Perrings et al. (1995) tells us that this notion of ecological resilience has increasingly come to represent an integral part of the academic debate about conservation-related issues. In this context, resilience—or resilience of the second kind—refers to “. . . the amount of disturbance that can be sustained [by an ecosystem] before

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a change in system control or structure occurs" (Holling et al. 1995, p. 50). This definition tells us that the resilience of an ecosystem is closely related to its stability. Consequently, the aim of conservation policy should be to take those steps that enhance ecosystem stability. Put differently, prudent conservation policy should *not* focus on the loss of genetic information but, instead, on the loss of ecosystem resilience.

Despite the significance of the concept of resilience, there are very few quantitative studies of resilience. In particular, with one exception, there do not appear to be any formal characterizations of resilience that link resilience to the number of species in an ecosystem. For instance, consider the work of Perrings (1991). The emphasis in this paper is not on resilience *per se* but on environmental control. Consequently, no formal definition of resilience is provided; instead, Perrings models resilience by introducing an ecological sustainability constraint. Common and Perrings (1992) and Perrings (1996) do provide formal definitions of resilience. These definitions essentially say that an ecosystem is resilient as long as the maximum perturbation that can be sustained by the state variables of this system lie in a certain neighborhood of an equilibrium. While these definitions do provide a link between resilience and ecosystem stability, they do not explicitly provide any link between resilience and the number of species in an ecosystem. However, the work of Schindler (1990) and Holling (1992) has shown that the resilience of ecological functions is intimately related to the *number* of substitute species in an ecosystem that can perform those same functions. Consequently, it is important to link definitions of resilience explicitly to the number of species in an ecosystem.

Recently, Batabyal (1997) provided such a definition of resilience. This definition equates resilience with the expected value of S , where S denotes "... the number of shocks that are required

for *all* the ecosystem species to perish” (Batabyal 1997, p. 5, emphasis added). It is clear that this definition does succeed in linking resilience to the number of species in an ecosystem. What is less clear is why should the resilience of an ecosystem depend on *every* species in that ecosystem.

Given the limited attention that has been accorded to the quantitative dimension of the notion of resilience, and the undeniable significance of this concept for the appropriate design of conservation policy, this paper has two objectives. The first objective is to use renewal theory—see Ross (1993, pp. 303-50), Ross (1996, pp. 98-162), and Wolff (1989, pp. 52-147)—to provide a characterization of resilience as a stationary probability. This characterization proposes that we think of resilience in terms of the survival of a *subset* of the set of all species in an ecosystem. We recognize that for any specific ecosystem, this subset may equal the set of all species. The second objective is to use this renewal theoretic characterization to study the question of the optimal number of species that should be conserved.

2. A Probabilistic Characterization of Resilience

Consider a stylized ecosystem that consists of n species, where $n \in \mathbb{N}$. Economic activities, such as agriculture, fishing, and grazing, affect the various species of this ecosystem. In particular, excessive economic activity of the above kind will result in the death of one or more of these species. We are referring to death literally and figuratively. In particular, we have two cases in mind. In the first case, species numbers have dwindled to such an extent that preventive policy measures, such as regulations on the nature of fishing equipment and moratoriums on grazing, are put in place to ensure that literal death (extinction) does not occur. This is the case of figurative death. In the second case, some species may die literally. Here we suppose that an ecosystem manager can

transfer this or a closely related species to our ecosystem from some other ecosystem. This second case includes the localized deletion of species. Unique species fall into the first case.

Suppose that independent of the survival of other species, the i^{th} species, $i \in [1, n]$, is alive for a time with distribution function $F_i(\bullet)$. This distribution function has mean α_i . Suppose that independent of the survival times, the i^{th} species, $i \in [1, n]$, is dead or absent from the ecosystem for a time with the distribution function $G_i(\bullet)$. Let the mean of this distribution function be β_i . The death times of the various species are stochastic, because the rate at which species regenerate or recuperate is generally a stochastic function of environmental variables and the preventive policy measures that have been put in place by an ecosystem manager.

There will generally be some uncertainty in the current state of ecological knowledge as to how many species are actually necessary for our ecosystem to be stable. Let this number be m . We shall model this ecological uncertainty by allowing m to be any integer between 1 and n . Our task now is to compute the resilience of our ecosystem. Because resilience is a stationary probability, we are interested in computing $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}$, where $A(t)$ denotes the number of species that are alive at time t .

The reader will note that for each species in our ecosystem, the process of being alive and then dying constitutes an alternating renewal process. Consequently, the stationary probability that species i is alive is

$$p_i = \frac{\alpha_i}{\alpha_i + \beta_i}. \quad (1)$$

From equation (1) and from our independence assumption we can determine the resilience of our ecosystem. We get

$$\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\} = \sum_V \left[\prod_{i \in V} \left\{ \frac{\alpha_i}{\alpha_i + \beta_i} \right\} \prod_{i \in V^c} \left\{ \frac{\beta_i}{\alpha_i + \beta_i} \right\} \right], \quad (2)$$

where the summation in this equation is taken over all the $\binom{n}{m}$ subsets V that are of size m .

The expression in equation (2) is our probabilistic characterization of ecological resilience. The reader will note that we have equated the resilience of our ecosystem with the long-run probability that the number of species that are required for stability (m) will, in fact, survive the effects of continued economic activity. More specifically, this measure of resilience depends on the number of species in the ecosystem (n), on (m), and on the means of the survival time and the death time distribution functions (α_i , β_i). In order to operationalize this measure of resilience, it will be necessary to (i) have an estimate of the number of species in the ecosystem; (ii) determine the number of key species, i.e., those that are necessary for ecosystem stability; and (iii) estimate the means of the survival time and the death time distribution functions.

To fix ideas, we now provide an example and an extension of the methodology that we have used in this paper to compute the resilience of our ecosystem. The example illustrates how our measure of resilience can actually be used. The extension shows how an ecosystem manager can compute the resilience of our ecosystem at any finite point in time.

2a. An Example and an Extension

Suppose that there are $n = 3$ species in our ecosystem and that, in order for this ecosystem to be stable, $m = 2$ of these species must survive. Further, suppose that the survival times and the death times are exponentially distributed for all the species in our ecosystem. In particular, let

$\gamma = 0.4$ be the rate of the $F_i(\bullet)$, $\forall i$, and let $\delta = 0.6$ be the rate of the $G_i(\bullet)$, $\forall i$. Our task now is to determine the resilience of this ecosystem, i.e., to determine $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}$.

It is important to note that, in this case of exponential survival and death times, the life/death status of any species constitutes a two-state, continuous time Markov chain. If we let state 1 correspond to being alive, then the transition probability $P_{11}(t)$ is given by

$$P_{11}(t) = \frac{\gamma e^{-(\gamma+\delta)t} + \delta}{\gamma + \delta} = 0.4e^{-t} + 0.6. \quad (3)$$

Using this transition probability, an expression for the resilience of this ecosystem can be obtained.

We get

$$\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\} = \lim_{t \rightarrow \infty} \binom{n}{m} \{P_{11}(t)\}^m \{1 - P_{11}(t)\}^{n-m}. \quad (4)$$

Now using equation (3), $n = 3$ and $m = 2$ in equation (4), we get 0.432 as the numerical value for this ecosystem's resilience. This completes the example.

To determine the transient resilience of this ecosystem, i.e., the resilience at any time t , other than at $t = \infty$, an ecosystem manager will want to compute $\text{Prob}\{A(t)=m\}$. From equation (4), we see that this probability is given by

$$\text{Prob}\{A(t) = m\} = \binom{n}{m} \{P_{11}(t)\}^m \{1 - P_{11}(t)\}^{n-m}. \quad (5)$$

For the special case of this subsection, equation (5) tells us how this paper's characterization of resilience can be generalized to cover finite planning horizons. A more general discussion of the computation of the transient resilience of an ecosystem is contained in Batabyal (1998).

We now use $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}$ to study an aspect of the optimal species conservation question in a framework in which an ecosystem manager/social planner takes the ecological and the economic aspects of the question into account.

3. Resilience and Conservation

In recent times, the question of what to conserve has been the subject of a considerable amount of ecological and economic research. In particular, Peters, Gentry, and Mendelsohn (1989), Balick and Mendelsohn (1992), Simpson and Sedjo (1996), and Batabyal (1997) all analyzed different aspects of this conservation question. While these papers have certainly advanced our understanding of the many and varied intricacies of the conservation question, this research has *not* considered the nexus between ecological resilience and conservation. Consequently, in what follows, we shall analyze a simple model of optimal species conservation that incorporates the ecological and the economic dimensions of the question.

Suppose that our ecosystem provides economic and ecological benefits to society. The economic benefits include the flow of services provided by activities such as biodiversity prospecting, grazing, and hunting. Clearly, the continuance of these benefits depends on the resilience of the ecosystem. Consequently, we shall suppose that society derives benefits from the resilience of this ecosystem. To this end, let $B[\vec{x}, \lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}]$ denote society's benefit function. The vector $\vec{x}=(x_1, \dots, x_r)$ denotes the r possible economic activities that society may engage in and $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}$ is the resilience of the ecosystem. We shall suppose that $B[\bullet, \bullet]$ is strictly concave and strictly increasing in both of its arguments. In other words, increasing the level

of economic activities and/or the resilience of the ecosystem enhances social benefits, but at a decreasing rate.

Economic activities are costly to undertake, and these activities have varied effects on the n species in our ecosystem. Consequently, there is a cost involved in conserving these species. Let $C_1[\bar{x}]$ denote the cost of engaging in economic activities and let $C_2[n]$ denote the cost of conserving the n species. We assume that these two cost functions are strictly convex and strictly increasing in their arguments. This means that an increase in either the level of economic activity or the number of species will lead to higher costs at an increasing rate.

Finally, suppose that our ecosystem manager solves his optimization problem subject to the resilience constraint $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\} \geq \bar{P}$. This constraint says that in solving his optimization problem, the ecosystem manager cannot allow the resilience of the ecosystem to fall below an exogenously given standard P . P , which is bounded away from zero, can be interpreted as a “safe minimum standard.” Our ecosystem manager’s problem can now be formally stated. This manager solves

$$\max_{\bar{x}, n} B\left[\bar{x}, \lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}\right] - C_1[\bar{x}] - C_2[n]. \quad (6)$$

subject to

$$\lim_{t \rightarrow \infty} \text{Prob}\{A(t) = m\} \geq \bar{P}. \quad (7)$$

As in Batabyal (1996, 1997), problems (6)-(7) is a mixed integer programming problem. This is because x is a continuous decision variable (by assumption) and because n is an integer decision variable. In order to apply the calculus to this problem, we shall interpret n as the rate of species conservation, and we shall suppose that we have a continuous approximation of $\lim_{t \rightarrow \infty} \text{Prob}\{A(t)=m\}$

in n . Then, omitting the complementary slackness conditions, the relevant Kuhn-Tucker optimality conditions for problem (6)-(7) are

$$\frac{\partial B[\bullet, \bullet]}{\partial x_q} - \frac{\partial C_1[\bullet]}{\partial x_q} \leq 0, \quad x_q \geq 0, \quad q = 1, \dots, r, \quad (8)$$

and

$$\frac{\partial B[\bullet, \bullet]}{\partial \{\lim_{t \rightarrow \infty} \text{Prob}\{A(t) = m\}\}} \frac{\partial \{\lim_{t \rightarrow \infty} \text{Prob}\{A(t) = m\}}{\partial n} - \frac{dC_2[\bullet]}{dn} \leq 0, \quad n \geq 0. \quad (9)$$

Equation (8), the economic first-order condition, says that in general each of the r economic activities should be pursued up until the point where the marginal social benefit from this activity equals its marginal social cost. Of greater interest is equation (9), the ecological first-order condition. This equation has implications for species conservation. The equation says that, in the general case, our ecosystem manager should conserve species at a rate so that the marginal social cost of conservation equals the marginal social benefit. Note that the marginal social benefit is the product of two terms; the first term captures the effect of a marginal increase in resilience on social benefit, and the second term captures the effect of an incremental increase in the rate of species conservation on ecological resilience. The reader will note that because the concept of ecological resilience is, *inter alia*, a function of the number of species in an ecosystem, it is possible to study the question of optimal species conservation in a way that considers the ecological and the economic aspects of the problem jointly.

4. Conclusions

In this paper we provided a new characterization of the concept of ecological resilience. This characterization depends on the number of species in an ecosystem, on the number of species that

are necessary for stability, and on the expected values of the survival and the death time distribution functions. We then used this characterization to study the question of optimal species conservation.

We have seen that in order to operationalize this paper's measure of resilience, it will be necessary to estimate the number of species in the ecosystem, determine the number of species that are necessary for stability, and estimate the means of the survival and the death time distribution functions for the different species.

The analysis of this paper can be extended in a number of different directions. In what follows, we suggest two possible extensions. The characterization of resilience provided in this paper did not explicitly allow for the differential impact of economic activities on the species of our ecosystem. The varying impacts of alternate kinds of economic activity would presumably make the mean of the survival time distribution function time dependent. Nor did this paper's characterization of resilience consider the possibility that the substitutability in the performance of ecological functions will typically lead to some species redundancy. As indicated earlier, the work of Schindler (1990) and Holling (1992) tells us that the resilience of ecological functions in ecosystems is generally an increasing function of the number of substitute species that can perform those functions.

Formal studies of resilience that incorporate these aspects of the problem into the analysis will provide richer and more realistic characterizations of resilience. Further, such studies will permit more elaborate analyses of the connections between species conservation and ecological resilience.

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